

GROWTH RATES OF THE SEA SCALLOP, *PLACOPECTEN MAGELLANICUS*, DETERMINED FROM THE $^{18}\text{O}/^{16}\text{O}$ RECORD IN SHELL CALCITE

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ABSTRACT

Present age determination techniques for the sea scallop, *Placopecten magellanicus* (Gmelin), rely on the subjective interpretation of lines on the shell exterior as representing periods of annual growth. This study compares scallop age and growth estimates from the external line method with a stable isotope technique. The oxygen isotopic records from serially sampled carbonate powders taken from two scallop specimens collected alive off the Virginia coast show annual cycles which closely approximate the isotopic composition predicted as a function of observed salinity and temperature. Since these annual isotopic cycles are controlled by physical-chemical processes, they provide an independent time scale for age and growth rate determination. Growth rates determined from the isotopic records are roughly twice those estimated from the external line method and from a published average growth curve for *Placopecten magellanicus*.

INTRODUCTION

The sea scallop, *Placopecten magellanicus* (Gmelin), is an important economic resource for the New England and Atlantic Canada fisheries, providing the fourth highest income from landings (Bourne, 1964; Serchuk *et al.*, 1979). Average annual production from combined U. S. and Canadian catches is on the order of 13,000 metric tons of meats (Serchuk *et al.*, 1979). Harvestable populations of sea scallops occur from St. Lawrence Bay to the Virginia-North Carolina continental shelf just north of Cape Hatteras (Posgay, 1957; Merrill, 1962). Sea scallops in the northern portion of the range inhabit water depths from approximately one meter below mean low tide to just deeper than 100 meters on the continental shelf (Dickie, 1955). The more southerly populations inhabit increasingly deeper waters. In the Virginia Bight, the southern extreme of their range, sea scallops are confined to 40–100 meter water depths (Merrill, 1971), presumably in response to lethal summer temperatures above 20–23°C (Dickie, 1958) in shallower waters.

The considerable economic importance and heavy fishing of sea scallop stocks underscore the need for accurate age and growth rate estimates for this species. Such information is vital if the sea scallop fishery is to be managed effectively. The techniques which are presently employed for age determination of the sea scallop rely on the interpretation of lines visible on the exterior of the shell or on the hinge ligament (Stevenson and Dickie, 1954; Merrill *et al.*, 1965). Based primarily on mark and recovery studies, several pectinids, including *Placopecten magellanicus*, deposit annual rings or growth lines in late winter or early spring (Stevenson and Dickie, 1954;

Taylor and Venn, 1978; Serchuk *et al.*, 1979; Paul, 1981). Scallops deposit calcium carbonate in the form of calcite to the shell margin in concentric increments. During the warmer months of the year, while the scallops are growing rapidly, the distance between consecutive increments is relatively wide (Stevenson and Dickie, 1954; Mason, 1957; Taylor and Venn, 1978). As growth slows during the winter and early spring, the growth increments are crowded together, forming what appears to be a concentric line or ring on the shell (Fig. 1).

The interpretation of external lines as representing years of growth for an individual specimen is often complicated by numerous disturbance or shock rings. Sea scallops are notably sensitive to physical disturbances and sudden changes in environmental conditions such as sharp temperature or salinity changes, or storm-related turbulence (Merrill *et al.*, 1965). In response to strong stimuli, scallops retract the mantle and cease calcification along the shell margin. This action leaves a noticeable line after shell growth resumes. Distinguishing annual lines from disturbance lines macroscopically is frequently difficult and often very subjective (Stevenson and Dickie, 1954; Merrill *et al.*, 1965). Other shell characteristics, such as seasonal variation in shell color, convexity of the shell profile, and activity of boring organisms, may provide some information for the interpretation of external lines (Merrill *et al.*, 1965). However, these additional methods are still very subjective and are not conclusive. In view of the uncertainties involved in the accurate interpretation of growth rings, additional methods of establishing the periodicity of these features have been pursued in other species of molluscs. Principal among these efforts has been the investigation of stable isotope variations across shell increments (*e.g.*, Yavnov and Ignat'ev, 1979; Jones *et al.*, 1983).

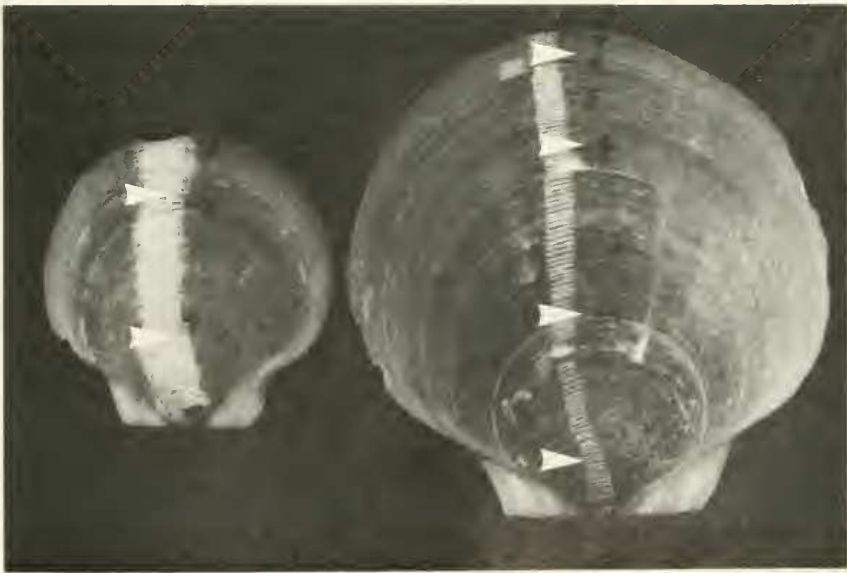


FIGURE 1. Two specimens of *Placopecten magellanicus*, PM10 (left) and PM26 (right), used for isotopic analyses. Years of growth estimated from external lines are marked on the shell with corresponding year number. Position of shell margin for each summer of growth as determined from the isotopic profiles are indicated by white arrows. Grooves drilled to collect carbonate powder samples are visible on the shell exterior.

Application of stable isotopic methods to mollusc studies

This study utilizes the ratio between the stable isotopes of oxygen, ^{18}O and ^{16}O , in scallop shell carbonate to monitor ambient water conditions during shell deposition, and ultimately to make interpretations about shell growth. Because of the thermodynamic behavior of the oxygen isotopes in chemical reactions, the ratio of $^{18}\text{O}/^{16}\text{O}$ in the product is a function of the $^{18}\text{O}/^{16}\text{O}$ ratio of the reactants and the temperature at which the reaction occurred (Urey, 1947). During the deposition of shell carbonate by a mollusc, this isotopic fractionation is controlled by the $^{18}\text{O}/^{16}\text{O}$ ratio of the water in which the animal is living and the ambient temperature during shell deposition. With a constant $^{18}\text{O}/^{16}\text{O}$ ratio for water, relatively fewer ^{18}O atoms are incorporated into shell carbonate in the warmer summer months ("lighter" isotopic values) and proportionately more ^{18}O atoms are incorporated in the cooler winter months ("heavier" isotopic values). The temperature control on the fractionation of oxygen isotopes is a function of the reaction kinetics and in molluscs is, for the most part, independent of physiological processes (Epstein and Lowenstam, 1953; Epstein *et al.*, 1953; Jones *et al.*, 1983).

The isotopic composition of shell carbonate is also a function of the $^{18}\text{O}/^{16}\text{O}$ ratio of the water. The water $^{18}\text{O}/^{16}\text{O}$ is a conservative property and may be related to salinity in that sea water is isotopically heavier (relatively more ^{18}O) than freshwater (Epstein and Mayeda, 1953; Fairbanks, 1982). Shell carbonate deposited by molluscs living in marine conditions will be isotopically heavier than shell carbonate deposited under freshwater conditions (Epstein *et al.*, 1953; Keith *et al.*, 1964; Eisma *et al.*, 1976).

The controlling factors of water $^{18}\text{O}/^{16}\text{O}$ and temperature have been quantified and related to shell carbonate isotopic composition in the calcite paleotemperature equation (Epstein *et al.*, 1951; Epstein *et al.*, 1953). The principal application of this equation is to calculate temperature of formation from a known carbonate isotopic value when water isotopic composition is known or can be reasonably estimated. Epstein *et al.* (1953) emphasize that seasonal temperature cycles produce significant variations in isotopic composition within the shell. By sequentially sampling a mollusc shell at closely spaced intervals (approximately 1 mm), it is possible to check for seasonal changes in the $^{18}\text{O}/^{16}\text{O}$ ratio and compare these cycles with the shell growth record. Information obtained by sequential sampling of mollusc shells has allowed the interpretation of annual growth patterns (Wefer and Killingley, 1980; Cochran *et al.*, 1981), periodicity of growth increment formation (Horibe and Oba, 1972; Williams *et al.*, 1982; Jones *et al.*, 1983), and correlation of the shell isotopic record with upwelling events (Killingley and Berger, 1979), seasonal productivity changes, and thermocline development (Arthur *et al.*, 1983).

Hydrographic conditions of the study area

Hydrographic data obtained from 40 to 60 meter water depths in the shelf area near the collection site of specimens PM10 and PM26 were averaged by month for the years 1975 to 1979, which represent the growth period of the specimens. The area of the mid-shelf from which the scallop specimens were collected is essentially full marine with mean salinity of 33.7‰ and an average annual salinity range from 32.7 to 34.7‰ (unpublished data from NOAA-NODC; Nickerson and Mountain, 1983). A certain degree of seasonality is associated with salinity in that highest salinity values occur in the spring and fall, while lowest salinity values occur during mid-summer (Fig. 2). Occasional short-term deviations occur from this average trend, most probably in response to extreme precipitation or local hydrographic fluctuations.

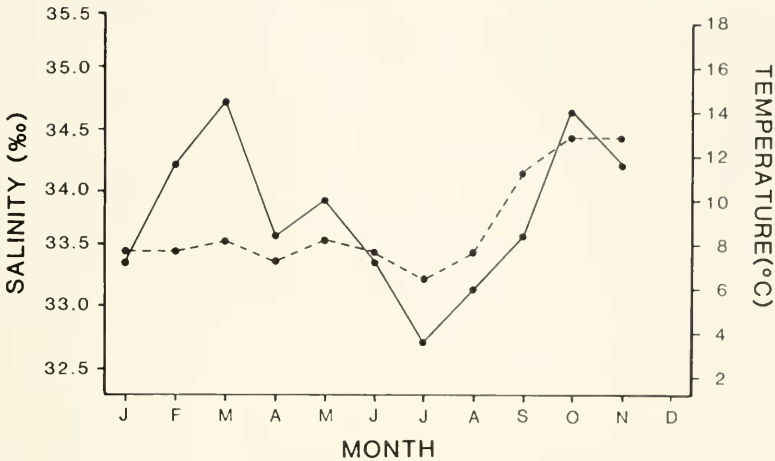


FIGURE 2. Mean monthly bottom water salinity (solid line) and temperature (dashed line) for areas of the Virginia Bight continental shelf with water depths between 40 and 60 meters. Data obtained from NOAA-NODC and Nickerson and Mountain (1983) are summarized for the years 1975–1979.

Average monthly bottom water temperatures for the same area range from approximately 6.0°C to a maximum of approximately 13.0°C. Extreme temperatures may be 2 or 3°C on either side of the average range, dipping to 4°C or rising to 16°C. Throughout most of the winter, spring, and early summer, average bottom water temperatures remain below 8.0°C (Fig. 2). Beginning in late summer and continuing through the fall, bottom water temperatures steadily increase to an annual maximum. An abrupt temperature drop with the onset of winter is followed by a fairly constant low temperature. As in the case of yearly salinity variations, short-term excursions in temperature also occur throughout the year, probably caused by local hydrographic events.

Predicted isotopic composition of shell calcite

The isotopic composition of shell calcite was predicted using: (1) an unpublished regression equation relating the water $\delta^{18}\text{O}$ to salinity for the Virginia Bight (R. G. Fairbanks, pers. comm.), (2) the average bottom-water salinity and temperature observations, and (3) the calcite paleotemperature equation (Epstein *et al.*, 1953). The predicted $\delta^{18}\text{O}$ of calcite can be estimated by solving the paleotemperature equation (Epstein *et al.*, 1953) using the quadratic formula, such that:

$$\delta^{18}\text{O}(\text{calcite}) = \delta^{18}\text{O}(\text{water}) + [(4.38 - \sqrt{19.18 - 0.4(16.9 - T)})]/0.20$$

where T = temperature in degrees C. Temperature observations and water $\delta^{18}\text{O}$ estimates from salinity observations were substituted into this derivation of the paleotemperature equation to predict the average oxygen isotopic composition of shell calcite deposited during each month of the year.

For areas of the Virginia Bight continental shelf with water depths between 40 and 60 meters, the predicted annual isotopic record from scallop shell calcite is as shown in Figure 3. A distinct seasonality is evident with the lightest isotopic values of approximately 0.5‰ occurring in the late summer and early fall, and the heaviest values of approximately 2.5‰ occurring in the winter. Since the curve is based on average hydrographic conditions, any given year of actual conditions may deviate

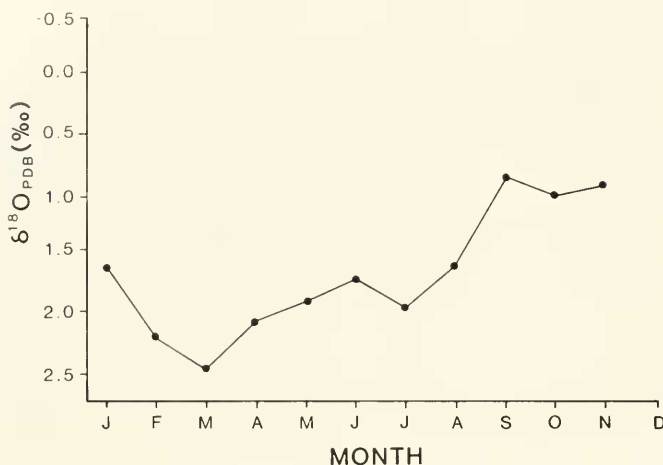


FIGURE 3. Predicted average monthly $\delta^{18}\text{O}$ values for scallop shell calcite. Shell carbonate isotopic composition was estimated using average monthly salinity and temperature values (Fig. 2) and the calcite paleotemperature equation (Epstein *et al.*, 1953). A distinct seasonality is evident, with lightest $\delta^{18}\text{O}$ values in the late summer and heaviest values in the winter and early spring.

somewhat from this predicted curve, and actual seasonal extremes may be somewhat greater. The short-term temperature and salinity excursions, which are not uncommon on the shelf, would be expected to show up in the shell isotopic record as deviations from the annual trend. However, the seasonal cycle should still be the major signal recorded in the shell carbonate of the scallop, as has been demonstrated for other mollusc species (Wefer and Killingley, 1980; Williams *et al.*, 1982; Jones *et al.*, 1983).

MATERIALS AND METHODS

Living specimens of *Placopecten magellanicus* used in this study were collected by National Marine Fisheries Service (NMFS) personnel during the 1979 yearly shellfish assessment survey. Isotopic analyses were performed on two specimens which were collected alive on 21 May 1979 from a station at 57 meters water depth approximately 90 km off the coast of Virginia ($37^{\circ}15'\text{N}$, $74^{\circ}45'\text{W}$). These two specimens (PM10, PM26) were chosen from a group of thirty because the exterior of both shells showed no evidence of boring or extensive erosion. Estimation of the yearly growth for each individual was made by NMFS personnel using lines on the shell exterior in a method described by Merrill *et al.* (1965). Indelible marks representing estimated years of growth were placed on each shell by NMFS personnel, and were later used for comparison with the growth interpretation based on the stable isotope record.

Both PM10 and PM26 specimens were prepared for isotopic analysis by first lightly grinding the exterior of the shell to remove the periostracum and any foreign debris. Discrete samples of carbonate powder were then drilled from the outer shell layer using a 0.5-mm dental drill bit. The calcium carbonate powders were collected in a series by drilling consecutive grooves parallel to shell growth increments from the umbo to the ventral margin along the axis of maximum growth. Samples were taken only from the outer prismatic shell layer which is deposited sequentially along the shell margin during the growth of the scallop. Care was taken to avoid the inner shell layer which is deposited in thin sheets over existing calcite. Any given point of

the inner shell layer will be composed of calcium carbonate deposited over an extended period of time instead of the single time slice represented by the overlying prismatic layer.

The stable isotopic composition of the shell powders was determined using standardized techniques (Williams *et al.*, 1977; Jones *et al.*, 1983). Approximately 0.5 mg of each carbonate sample was first roasted *in vacuo* at 380°C for one hour to remove any remnant of the organic matrix. Each roasted sample was then reacted in purified phosphoric acid at 50°C using a technique modified from McCrea (1950). The oxygen and carbon isotopic compositions of the evolved carbon dioxide gas were determined on a VG Micromass 602-D mass spectrometer. By convention, the isotopic values are recorded relative to the carbon dioxide gas derived from the Pee Dee Belemnite (PDB) standard carbonate powder (Epstein *et al.*, 1953) in conventional delta notation (δ , ‰). Analytical precision was ± 0.10 ‰ for prepared samples.

RESULTS

Specimen PM10, with a shell height of 75 mm, was estimated by NMFS personnel to have completed three years of growth and begun shell deposition in a fourth year. This age determination was based on an interpretation of the external growth lines represented diagrammatically in Figure 4. The millimeter scale on the horizontal axis relates the position of these external lines to shell height (as measured from the umbo to the margin) and the position of each carbonate powder sample drilled from the shell. Isotopic determinations were made on 46 discrete powders secured from the shell of specimen PM10. The oxygen isotope data (see Krantz, 1983 for data) are plotted in Figure 4 with the $\delta^{18}\text{O}$ scale reversed so that lower δ values, representing "warm" isotopic temperatures, are at the top of the vertical scale.

The oxygen isotope record from specimen PM10 exhibits two major cycles with approximately 2‰ variation between minimum and maximum $\delta^{18}\text{O}$ values (Fig. 4). The heaviest (most positive) $\delta^{18}\text{O}$ value in the record is +2.46‰ and the lightest (most negative) is +0.29‰. The $\delta^{18}\text{O}$ curve is roughly sinusoidal although occasional deviations of a few tenths of a per mil are observed from the trend.

As previously discussed, ambient temperatures during shell formation may be estimated from the calcite paleotemperature equation (Epstein *et al.*, 1953) using the $\delta^{18}\text{O}$ values of the individual carbonate samples and the $\delta^{18}\text{O}$ values of the water. As a first approximation, if one makes the simplifying assumption that changes in water $\delta^{18}\text{O}$ at the collection site are negligible, an average water $\delta^{18}\text{O}$ value of -0.25 ‰ (R. G. Fairbanks, pers. comm.) can then be used to estimate temperature during shell deposition. In this manner, the shell carbonate $\delta^{18}\text{O}$ values can be converted to temperature minima and maxima. Using this approximation, the minimum isotopic temperature recorded in the shell of PM10 is 6.5°C, the maximum is 14.6°C, and the average range is 7.5°C.

Specimen PM26, with a shell height of 126 mm was collected on the same day and from the same station as specimen PM10. NMFS personnel estimated the age of specimen PM26 to be seven years with the beginning of an eighth year of growth, again relying on the interpretation of external growth lines (Fig. 5). The $\delta^{18}\text{O}$ profile of PM26 shows four large amplitude cycles (Fig. 5) with approximately 2‰ variations occurring between minimum and maximum $\delta^{18}\text{O}$ values. Superimposed on these cycles are several smaller amplitude excursions of approximately 0.2 to 0.5‰. As with the oxygen isotope data from specimen PM10, the data from PM26 may be converted to isotopic temperature estimates using an average water $\delta^{18}\text{O}$ of -0.25 ‰. The minimum and maximum calculated temperature values vary from 5.7°C to 16.5°C, with an average range of 8.4°C.

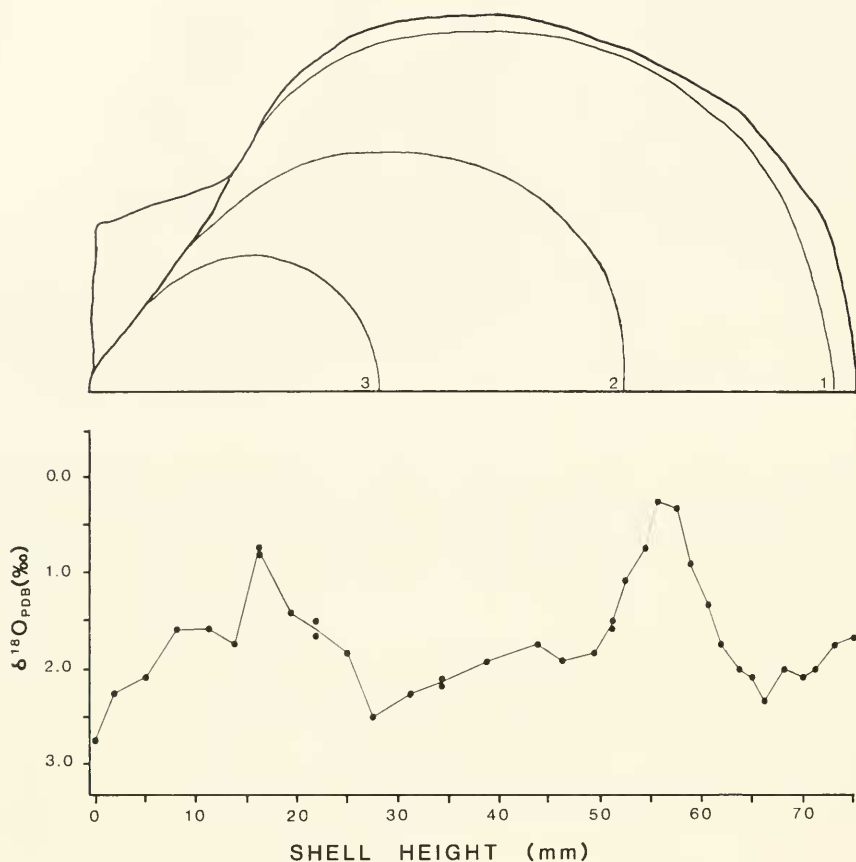


FIGURE 4. Position of external lines and shell carbonate oxygen isotopic record for the shell of specimen PM10. The external lines illustrated in the diagram are those interpreted by NMFS personnel as representing years of growth. These are numbered in reverse chronological order (line 1 is the most recently formed) to facilitate comparison with those on specimen PM26. The isotopic values of discrete sample powders are plotted with the $\delta^{18}\text{O}$ scale reversed so that lower δ values, which represent "warm" isotopic temperatures, are at the top of the vertical scale. The millimeter scale on the horizontal axis relates the position of the external lines and the position of individual carbonate powder samples to shell height.

DISCUSSION

Interpretation of observed oxygen isotope records

With the predictive model outlined previously, the oxygen isotope records obtained from the scallop shells may be interpreted as yearly cycles controlled by seasonal hydrographic conditions. The isotopic record from specimen PM10 is interpreted as showing two full years of growth with the beginning of a third year (Fig. 4). Specimen PM10 completed one year of growth at a shell height of 25 mm as determined by one full cycle in the isotopic record. Shell deposited from 0 to 10 mm gradually becomes isotopically lighter (more negative), representing late winter to late spring, and reaches an inferred late summer maximum temperature at approximately 15 mm shell height (Fig. 4). The seasonal trend continues into the late fall and early winter as represented by shell deposited from 15 to 25 mm. A second annual cycle

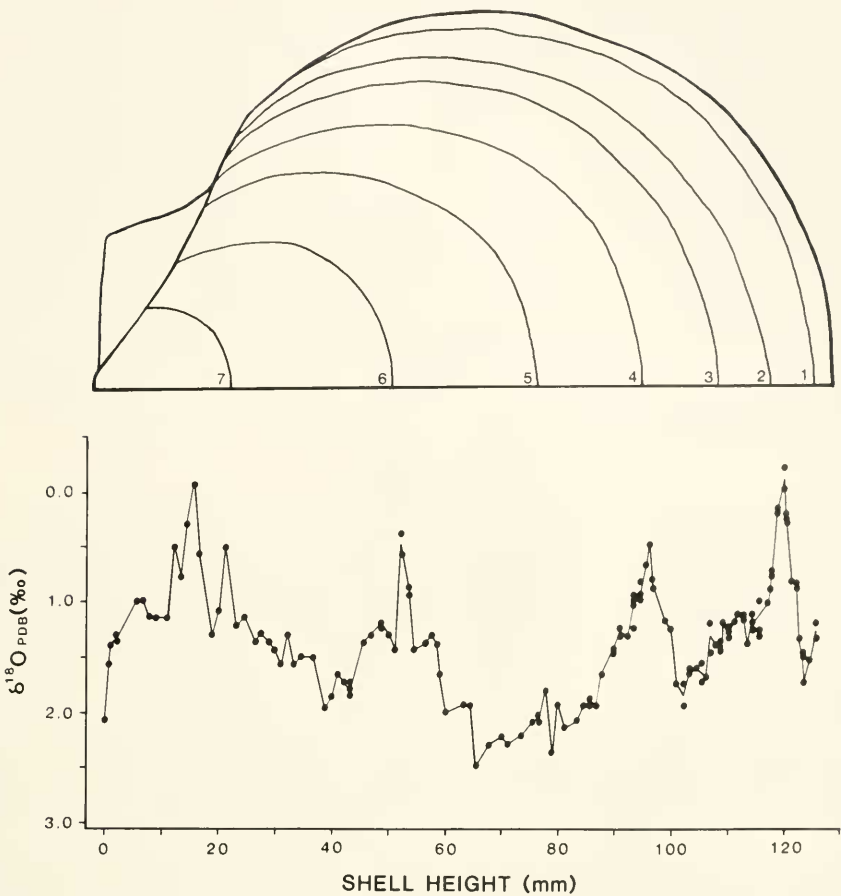


FIGURE 5. Position of external lines and shell carbonate oxygen isotopic record for specimen PM26. The external lines illustrated in the diagram are those which were interpreted by NMFS personnel as representing years of growth. As in Figure 4 for specimen PM10, the lines are numbered in reverse chronological order, and the oxygen isotopic values for shell carbonate samples are plotted with a reversed $\delta^{18}\text{O}$ scale.

begins at 30 mm, reaches a late summer temperature maximum at approximately 55 mm, and proceeds to a yearly minimum at 65 mm shell height. The beginning of a third annual cycle represented by the last 10 mm of shell and terminating at the ventral margin coincides well with the spring collection date (Fig. 4). Not only does the beginning of the isotopic cycle coincide with the seasonal hydrographic cycle, but the $\delta^{18}\text{O}$ values of samples taken from the shell margin are very close to the 1.7‰ value predicted by the model for May (Fig. 3). This agreement between isotopic "season" and collection date supports the validity of the isotopic record interpretation.

These results indicate a discrepancy between the three years of growth interpreted from the external lines and the two years of growth inferred from the $\delta^{18}\text{O}$ record. Further, the external lines, which are presumed to be deposited annually in the spring, appear to occur in various seasons according to the inferred seasonality of the isotopic profile. For example, external line number 3 was deposited in the fall of the first growth year, line 2 during summer of the second year, and line 1 the following spring (Fig. 4). In this particular specimen, there does not appear to be a consistent season

for external line formation, therefore, the assumption that these external lines represent true annual events does not appear to be valid.

As in the smaller specimen, the isotopic record from the shell of PM26 demonstrates what appear to be distinct, hydrographically controlled, annual $\delta^{18}\text{O}$ cycles (Fig. 5). Again, the four years of growth are recorded in PM26 by the cycles in the isotope curve. This age estimate is at variance with the seven years of growth interpreted from the external lines. The occurrence of external lines on the shell of PM26 appears to have a more consistent relationship to the seasonal $\delta^{18}\text{O}$ cycles than in PM10. Counting backwards from the ventral shell margin, and hence backwards chronologically, external lines 2, 4, 6, and 7 of specimen PM26 were deposited during late summer maximum temperatures (Fig. 5). A little more in line with the presumed deposition of annual lines in the spring by *Placopecten*, external lines 1, 3, and 5 appear to have been deposited in middle spring to possibly early summer. As in specimen PM10, the termination of the isotopic record at the shell margin is consistent with the spring collection date.

Comparison of the records from the two specimens

Since both scallop specimens were collected alive in 1979, calendar years may be assigned to years of growth by counting backwards from the shell margin (which represents the collection date). By assigning calendar years in this manner, the interpretation of the isotopic records and the external growth lines from the two specimens may be compared directly. In Figure 6 the shell records of specimens PM10 and PM26 are overlaid based on distance from the shell margin and on an interpretation of the isotopic record.

The cycles in the isotopic record of specimen PM26 which we interpret as representing the calendar years 1978 and 1979 do not include the isotopically heavy carbonate which the model predicts should be deposited during the winter. In comparison, the isotopic record for these same years from specimen PM10 includes carbonate isotopic values as heavy as those predicted by the model. Since other bivalves have been documented to slow or cease calcification during the winter (Taylor and Venn, 1978; Clark, 1979; Jones, 1980), it is reasonable to assume that the values "missing" from the isotopic record of specimen PM26 represent cessation of shell deposition. Similar interpretations have been proposed for the attenuation of cycles in the isotopic record for conchs (Epstein and Lowenstam, 1953; Wefer and Killingley, 1980) and surf clams (Jones *et al.*, 1983). The isotopic record of specimen PM10 is used in Figure 6 to represent the complete record for the years 1978 and 1979, while the isotopic record of specimen PM26 has been separated to illustrate periods of cessation of shell deposition. The first two years of growth in specimen PM26 appear to be relatively complete. However, the isotopic values representing the winter months of 1975–76 are slightly lighter than expected which may indicate lack of shell deposition for a short period. Alternatively, the winter of 1975–76 may have been slightly warmer than 1976–77, but this possibility can be confirmed without more complete hydrographic information.

Overall, the two major cycles in the isotopic record for specimen PM10 coincide well with the cycles from specimen PM26. The records from both shells have very similar amplitudes and absolute isotopic values. As previously discussed, the predicted $\delta^{18}\text{O}$ values demonstrate a distinct seasonality in varying from 2.5‰ in the winter to 0.5‰ in the late summer. The cycles in the isotopic records of both specimens fall almost exactly within the predicted range estimated from the hydrographic data. The isotopic temperature range of 5.7°C to 16.5°C calculated from shell calcite $\delta^{18}\text{O}$

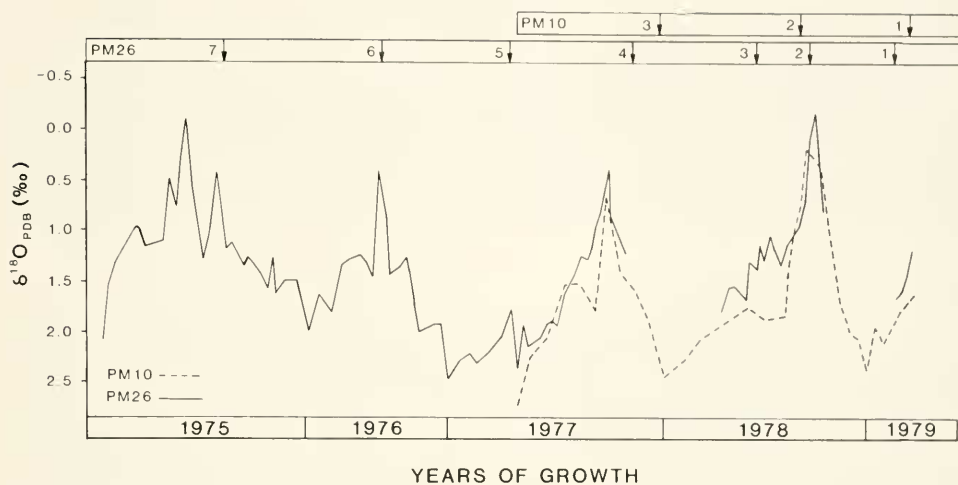


FIGURE 6. Comparison of the $\delta^{18}\text{O}$ records of specimens PM10 and PM26. The isotopic profile of specimen PM10 is represented by the dashed line, that of specimen PM26 by the solid line. Calendar years assigned to each annual cycle in the $\delta^{18}\text{O}$ records of each specimen comprise the horizontal axis. External lines interpreted as annual marks are represented for each specimen at the top of the diagram. Breaks in the record of specimen PM26 correspond to presumed curtailment of calcification by the scallop.

values corresponds well to the observed water temperatures for the area. The few excursions outside of the predicted range represent minimum and maximum temperatures which were probably dampened in the model by using hydrographic data which were averaged by month. These calculated temperatures also seem reasonable in that maximum temperatures fall below the reported lethal temperature of approximately 20°C (Dickie, 1958).

Seasons and years determined from the isotopic record allow correlation of growth lines between the two specimens and aid in evaluating possible mechanisms for line formation. External line 1 on the shell of specimen PM10 was formed in the spring before the collection date in May, 1979. Line 2 on specimen PM10 appears to correspond with line 2 on specimen PM26, both having been deposited in summer 1978 just prior to the annual temperature maximum. Similarly, growth lines 6 and 7 on specimen PM26 were deposited in middle to late summer of years 1976 and 1975 respectively.

The previously mentioned external lines appear to have been formed with little cessation of growth as evidenced by loss of "time" from the isotopic record. In contrast, external lines 1 and 4 in specimen PM26, and line 3 in specimen PM10 appear to coincide with periods of missing isotopic values. As was pointed out previously, two gaps in the isotopic record of specimen PM26 corresponding to the winters of 1978 and 1979 are interpreted as cessation of shell growth. Each of these gaps is marked by a line on the shell. On specimen PM10, line 3 coincides with a sudden shift in isotopic values, which suggests that it may be analogous to line 4 in specimen PM26 and was probably formed at approximately the same time. In each case, the specimens appear to have stopped or drastically slowed calcification in the fall and added no shell material during the winter, hence there are no isotopic values representing those periods. After this cessation of growth, specimen PM10 appears to have resumed calcification much sooner than PM26, which explains the difference in the two isotopic records for the early spring of 1978. Specimen PM10 apparently

did not curtail calcification in the winter of 1978–79, as evidenced by a fairly complete isotopic record for the period.

Sea scallops are sensitive to disturbance or abnormal changes in environmental conditions (Merrill *et al.*, 1965). External line 5 on the shell of specimen PM26 seems to coincide with anomalously light isotopic values during the early spring of 1977. The lighter than expected isotopic values were possibly the result of a low salinity event which may have eventually caused mantle retraction, shell closure, and a temporary halt to calcification.

Growth rate determinations

Since the isotopic composition of *Placopecten* appears to be controlled by seasonal hydrographic factors, the isotopic record from a shell should provide a useful time scale for determining rate of growth. The number of months from the beginning of shell deposition may be estimated for obvious seasonal peaks such as summer maxima and winter minima. This time scale may then be related directly to the positions on the shell of the respective samples. Constructed in this manner, a standard graph of shell height to years of growth (Fig. 7) illustrates that specimens PM10 and PM26 show an average rate of growth of approximately 35 mm per year (as interpreted from the isotopic record). The first two years of growth in both specimens show a very similar, approximately linear, growth rate even though they represent different calendar years. This supports the growth rate interpretation by suggesting a similar trend in ontogenetic development. For years two through four in specimen PM26, the rate of growth gradually slows, which is typical for many species of molluscs (Mason, 1957; Hallam, 1967; Jones *et al.*, 1978; Serchuk *et al.*, 1979).

The growth rates inferred from the isotope profiles of PM10 and PM26 can also be compared to the rates as determined using the external line aging technique (Fig. 8). Growth rate estimates based on the external lines would suggest that the two specimens grew approximately 20 mm per year for the first three years of growth. The larger specimen, PM26, shows a significant decrease in growth rate with age.

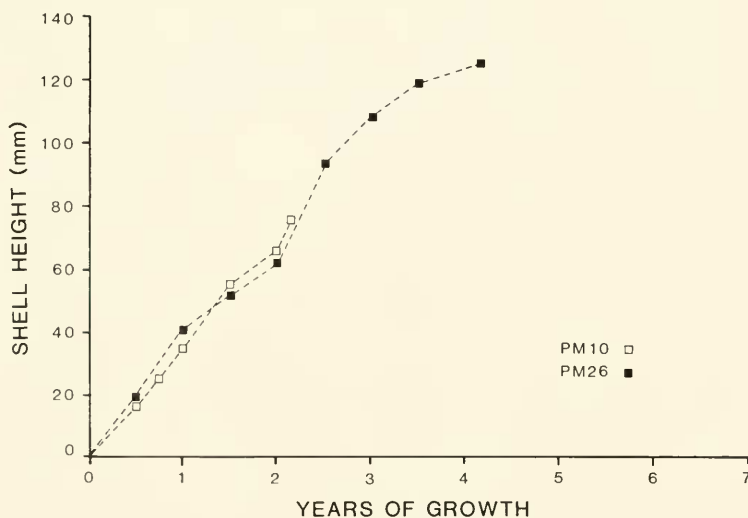


FIGURE 7. Growth rates of specimens PM10 and PM26 interpreted from the isotopic profiles. Points on each curve correspond to shell height at obvious seasonal peaks (summer maximum and winter minimum). Open squares represent shell heights for specimen PM10; closed squares represent specimen PM26.

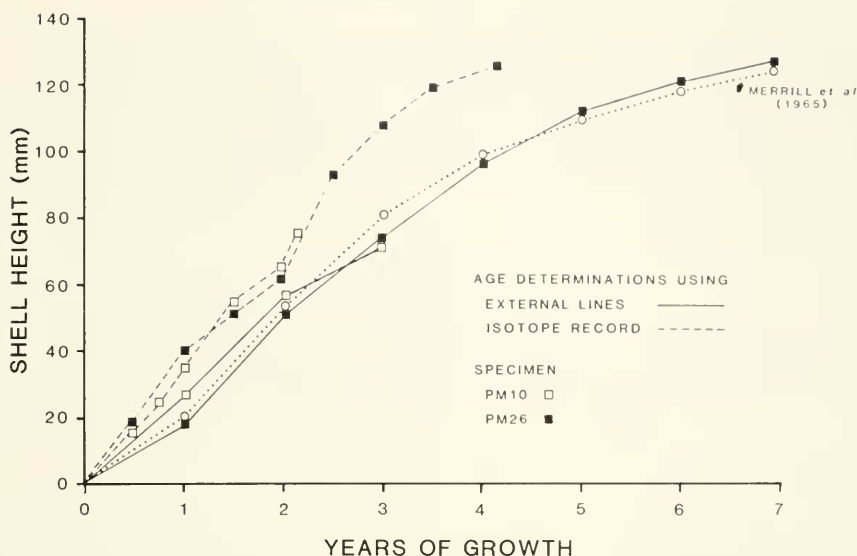


FIGURE 8. Comparison of growth rates determined from the external line technique and from the isotopic record. Growth rates for specimens PM10 and PM26 interpreted from the isotopic profiles are represented by dashed lines. Growth rates for the same two specimens determined from the external lines are represented by solid lines. Open squares indicate shell heights for specimen PM10; closed squares indicate specimen PM26. Dotted line illustrates an average growth curve for 351 *Placopecten* specimens aged using the external line method published by Merrill *et al.* (1965).

The growth rate estimates for both specimens fall very close to a curve constructed from average age/height data that Merrill *et al.* (1965) generated by estimating the age of 351 scallops using the external line technique. Although the growth rate estimates based on the external lines are internally consistent, they differ considerably from those interpreted from the isotopic record (Fig. 8). The growth rate determined from the isotopic record is roughly twice that from the external line method. This would be expected considering the discrepancy between the age (years of growth) estimates.

Migration

Results from previous tag-release studies suggest that sea scallops do not show any widespread or directed seasonal migration (Dickie, 1955; Posgay, 1963, 1981). The shell isotopic records presented here support this idea of limited movement. If the scallop specimens had migrated from either deeper or shallower water areas, the movement should have appeared as a significant change in the amplitude of the annual $\delta^{18}\text{O}$ cycles. In general on the continental shelf of the Virginia Bight, seasonal bottom water temperature fluctuations are greater in shallower water, and become progressively more dampened with increasing depth (Nickerson and Mountain, 1983). The isotopic record contained in shell carbonate, being controlled largely by ambient temperature, should also have a greater amplitude for a scallop living in shallower water. Taking into account the interruptions during calcification noted previously, specimens PM10 and PM26 have very similar isotopic amplitudes. This similarity in isotopic amplitude is seen in comparing individual cycles within the record of a single specimen, and in comparing the records of the two specimens. Therefore, it appears that the two scallop specimens, PM10 and PM26, remained in essentially the same depth habitat during their lives.

Implications for shellfisheries management

Methods presently used for the determination of age and growth rate in sea scallops rely on the interpretation of lines or rings on the shell exterior. Although some mark and recovery studies have shown that sea scallops produce an external line in the spring, lines are also produced during other times of the year, presumably in response to physical disturbance. This study demonstrates that the ratio of $^{18}\text{O}/^{16}\text{O}$ incorporated in the shell carbonate can be used to avoid the subjectivity of interpreting external lines as annual marks.

One particular advantage of using the isotopic record as an age determination tool in molluscs is the fact that the $\delta^{18}\text{O}$ -derived time scale is primarily controlled by the seasonal changes in hydrographic conditions. Because of this independent control, the interpretation is less subjective than distinguishing between shock lines and true annual lines on a scallop shell. From the evaluations performed in this study, external lines do not always form concurrently or consistently for all individuals in a scallop population. On the other hand, the shell isotopic composition should record the same annual cycles for the entire population. It should, however, be noted that the stable isotope method does not lend itself to use with large numbers of specimens, primarily because of the time and expense involved in the isotopic analyses. However, the technique does allow accurate age determination for small groups of specimens used for modeling periodic external line formation, growth rates, and other processes related to biomineralization.

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